SEXUAL SELECTION IN THE SOCORRO ISOPOD, *THERMOSPHAEROMA THERMOPHILUM* (COLE) (*CRUSTACEA: PERACARIDA*)

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Abstract. Females and parental males commonly discriminate among potential mates. Male discrimination is often assumed to be lacking in species with non-parental males. However, male competition in these species may favour male discrimination since indiscriminate matings may waste time and energy. Males in such species should attempt to maximize their fertilization rates; females in such species should mate only with males able to enhance female reproductive success. Males of the Socorro isopod, *Thermosphaeroma thermophilum*, engage in precopulatory guarding, preferring larger, more fecund females and females near a reproductive moult. Males also guard post-moult females. Large males prevail when usurping or resisting usurpation, and guard large females. Females may choose mates by selective resistance to insemination attempts.

Sexual selection operates in two contexts: (1) competition among members of one sex for access to members of the other sex (intrasexual competition), and (2) non-random selection of mates (intersexual selection). Intrasexual competition has long been accepted as an evolutionary force, and although initially disputed (Wallace 1889; Huxley 1938; Lack 1968), more recent discussions suggest that intersexual selection has had a significant role in evolutionary change (Williams 1966, 1975; Trivers 1972). Nevertheless, explanations for non-random mating unrelated to intersexual selection are numerous, and studies demonstrating adaptive mate choice are few (Thornhill 1980a). Thus the role of mate selection in effecting the differential reproduction of individuals remains somewhat uncertain.

Mate-discriminating ability is commonly associated with females because most females produce relatively small numbers of metabolically expensive gametes, and may invest considerable energy in parental care (Trivers 1972). Since female reproductive success depends on the number of offspring successfully reared, female choice ultimately prevents wasted reproductive effort. Mate selection may allow parental males to avoid cuckoldry (i.e. wasted reproductive effort: Ridley 1978; Smith 1979; Zenone et al. 1979; Thornhill 1980a), but most males (even parental ones) are assumed to lose little in indiscriminate matings since sperm may be abundantly and cheaply produced, and mating

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may require minimal energetic expense (Trivers 1972). However, male reproductive success frequently depends on the number of ova fertilized. Thus indiscriminate matings by males may waste time and energy (i.e. reproductive effort). Male discrimination is therefore expected in many animal species (see Parker 1970b, 1974).

Male guarding of females is thought to increase male confidence of paternity (Parker 1970a, 1974). Postcopulatory guarding should evolve when the ejaculate of the last male to mate has precedence over previous ejaculates, as in many insects (Parker 1970a). Precopulatory guarding should evolve when the ejaculate of the first male to mate has precedence over subsequent ejaculates, as in the spider mite, *Tetranychus urticae* (Potter et al. 1976; Potter & Wrensch 1978). Precopulatory guarding occurs in many crustacea (isopods, *Asellus intermedius* (Ellis 1961), *A. aquaticus*, *A. meridianus* (Manning 1975), *Ligia pallasii* (Carefoot 1973); cumaceans, *Mancocuma stellifera* (Guewuch & Croker 1973); brine shrimp *Artemia salina* (Lent 1977); lobsters, *Homarus americanus* (Atema et al. 1979)), although sperm precedence has not been investigated in these species. Anurans and most teleosts are not true copulators, but male territory defence while females spawn constitutes 'precopulatory' male guarding (Ridley 1978; Wilbur et al. 1978). The paternity of the first male to mate is frequently assured in these species. Both pre- and postcopulatory guarding occur in locusts, *Locusta migratoria migratoides* (Parker & Smith 1975). Such behaviour apparently ensures that a male is not merely the first male to mate, but also the only male to mate.
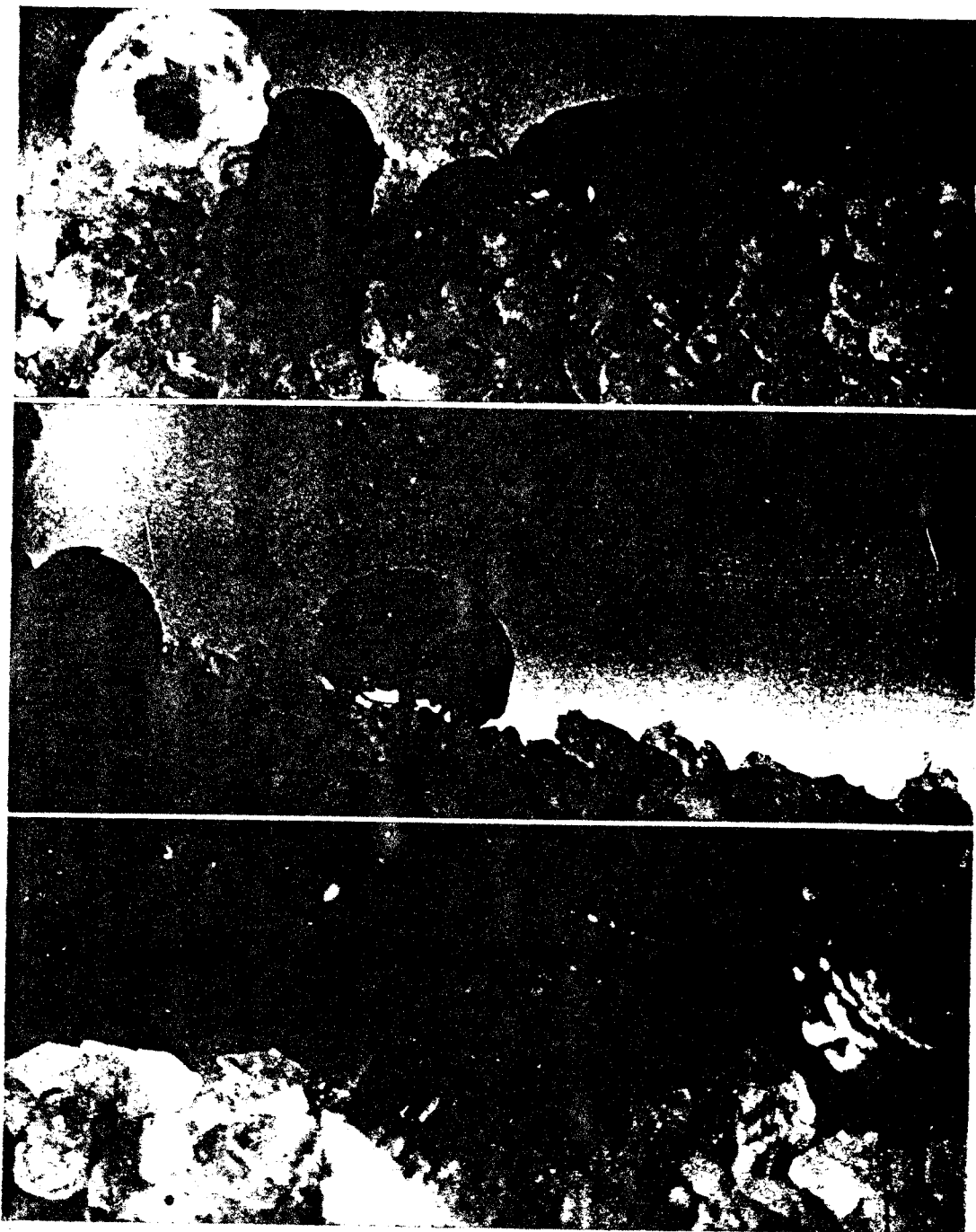
PLATE I

Fig. 1. (A) *Thermosphaeroma thermophilum*. Sexual dimorphism is pronounced; large individuals are male, small individual is female. (B) Females assume a spheroid shape when mounted by a male and remain in this position throughout assessment. (C) Guarding male (below) attacked by a single male (above). Note rolled-up female held by guarding male.

Males should apportion their total guarding time so as to maximize the rate at which they fertilize ova (Parker 1974). Time investment with one female necessarily limits the amount of time a male may spend seeking other females. Time investment may also impose physiological costs that limit future male reproductive success. Males should therefore guard only when doing so increases the expected yield of offspring with a particular female, e.g. by ensuring paternity, or when fewer offspring may be gained by further searching. The latter condition includes not only situations where receptive females are few, but also situations where males risk being excluded from females by more sexually competitive males. Male competition is often intense in species with male guarding behaviour (Parker 1974).

When access to females is determined by physical combat, male size is expected to contribute to mating success (Darwin 1874). Studies correlating male body size and male mating success include diverse taxonomic groups (insects, Thornhill 1980b; acariformes, Potter et al. 1976; Potter & Wrensch 1978; amphibians, Shine 1979, Howard 1978; lizards, Trivers 1976; snakes, Shine 1978; ungulates, pinnepeds, and primates, Alexander et al. 1979. To my knowledge, such documentation is very limited for crustacea and lacking for the Isopoda.

Three aspects of sexual selection in the isopod *Thermosphaeroma thermophilum* are documented in this paper: (1) male and female mate selection, (2) precopulatory guarding of females by males, and (3) male competition for mates.

Ecology of *T. thermophilum*

Thermosphaeroma thermophilum is a freshwater isopod, endemic to a single thermal effluent, Sedillo Spring, near Socorro, New Mexico (Shuster 1979). Most individuals are grey to reddish-brown in colour, with all exposed edges of the body tinged bright orange. Sexual dimorphism in this species is pronounced (Fig. 1A, Plate I): mature male body size (range = 8.0 to 91.0 mm^2, median = 18.0 mm^2, N = 776) is greater than mature female body size (range = 8.0 to 42.75 mm^2, median = 13.75 mm^2, N = 312) (Mann–Whitney U-test, P < 0.005).

This species has been classified as 'endangered' by the New Mexico Department of Game and Fish and by the U.S. Fish and Wildlife Service (Federal Register 1977). Much of the population is confined to a single, flat-bottomed concrete pool, 2.69 × 0.94 m. Water temperature is relatively constant throughout the year (31 to 33 C). The pool bottom is covered with 1 to 4 cm of finely divided substrate, and vegetation is limited to a thin film of filamentous blue-green algae that covers the pool walls. High densities (210 individuals/100 cm^2) of isopods in this arena-like area facilitated field observation. Predators are few or non-existent as fish do not inhabit the spring and the isopods attack and consume predaceous aquatic invertebrates. Water in the spring appears sufficiently deep (15 to 26 cm) to prevent predation by local birds. Birds were never observed feeding on isopods. Isopods feed primarily on blue-green algae as well as on leaves and detritus from nearby trees. Groups of isopods also rapidly locate and consume injured or dying conspecifics. Competition within these groups for access to carcasses appears intense. I have also observed apparently uninjured individuals attacked and devoured (N = 3, Shuster 1979). Attacked individuals were always smaller than attackers.

Males of this species guard females prior to insemination. My preliminary observations revealed four discrete male precopulatory behaviour patterns as follows: (1) Encounters, where males simply contact females and move on; (2) Assessments, where males grasp females and manipulate them for less than 15 s (manipulation consists of leg movements by the male along the body of the female, and males frequently turn onto their dorsal surface to accomplish this. Females assume a spheroid shape when mounted by a male and remain in this position throughout assessment); (3) Rejections, where males retain assessed females for longer than 15 s but less than 5 min; and (4) Guarding, where males retain females for longer than 5 min. I distinguished assessments and rejections because males that grasped females either rejected them almost immediately (within 15 s) or invested some guarding time before rejection. I also observed males grasping small stones and other males. Most frequently these interactions took about 15 s or less. Females held longer than 5 min were nearly always retained by males. Thus females held for more than 15 s but less than 5 min were considered attractive enough to warrant some male attention, but apparently were not considered suitable as mates, perhaps because higher-quality females were available. Males characteristically burrow beneath the substrate or seek cavities shortly after selecting a mate. Guarding males may be attacked by single males if pairs are not concealed. Copulation occurs after females are sequestered. The male assumes a ventral-to-ventral position with the

female and inserts a bifurcate penis into her genital openings. Female genitalia are located near the base of each fifth peraeonal (thoracic) leg. Females can effectively conceal these structures by rolling up, and thus appear capable of resisting insemination. Observed copulations ($N = 3$) lasted approximately 20 min, and the females were released by the males shortly thereafter (<4 min). Male precopulatory guarding can last as long as 10 days (see p. 704), but copulation was never observed in unsequestered pairs.

Female eubranchiate sphaeromatids such as *T. thermophilum* carry developing embryos in a ventral brood pouch, or marsupium, until young are ready to fend for themselves (Hansen 1906). Growth is indeterminate in this species, and sexual maturity is attained within 6 to 8 weeks. Most individuals live less than 1 year (Shuster 1979). Females are iteroparous and undergo cycles of both ovarian and hepatopancreas proliferation and reduction between reproductions (Table I). Each cycle consists of 3 distinct phases as follows: Phase 1 females have small, pale ovaries and no apparent hepatopancreas proliferation. This stage occurs immediately after young are released and prior to a sexual moult (a moult that initiates sexual receptivity). Phase 2 females are distinguished by ovaries that extend caudally to the fifth to seventh segment. Ovaries are yellow in colour but do not distend the venter, and individual ova are not distinct. Hepatopancreas development varies at this time but the organ is usually pale and indistinct. Females in phase 2 undergo a sexual moult. Phase 3 females have extensive ovarian development. Ovaries are

bright orange and extend the length of the peraeon (thorax), distending the venter. Ova are distinct. The hepatopancreas is branched and dark, and extends the length of the peraeon. Soon after phase 3, ova are shunted into the marsupium. Fertilization apparently occurs as ova are shunted and young are released in about 1 month.

General Methods

Collection of valid behavioural data under laboratory conditions is often problematic, as is the separation of sexually selected attributes from those evolving in other contexts. The simple habitat of *T. thermophilum* is easily recreated in the laboratory, and lacks strong selective pressures other than those imposed by the isopods themselves. The relative absence of complicating evolutionary contexts makes this system well suited for investigation of sexually selected behaviour and morphology.

With authorization by the New Mexico Department of Game and Fish, isopods were collected from Sedillo Spring in random sweeps along the bottom of the pool with a fine-mesh net (100×150 mm). Individuals were immediately placed in an insulated water jug containing spring water and transported to the laboratory, where they were transferred to 35-litre aquaria equipped with undergravel filters and several centimetres of finely divided gravel substrate. Water temperature was maintained at 31 C and a pinch of vegetable fish food (Tetra-min) was placed in each aquarium every 3 to 5 days. Algae usually appeared on aquarium walls and on the sub-

Table I. Characteristics of Female Reproductive Phases

	Reproductive phase		
	1	2	3
Relationship to a sexual moult	Premoult	Recently moulted or about to moult	Postmoult
Days after last brood*	0–7	8–15	16–40
Ovaries	Small, pale; extend to 3rd segment	Yellow; extend to 5th to 6th segment; do not distend venter; ova indistinct	Yellow to orange; extend the length of peraeon; distend ventner; ova distinct
Hepatopancreas	Not apparent	Varies; usually small, pale, indistinct	Extensive; dark, distinct branches
Cuticle	Dull; marsupial lamellae from previous brood may be visible*	Moult; cuticle lustrous after moult; marsupial lamellae indistinct	Lustrous to dull; marsupial lamellae distinct

*Applies only to non-virgin females.

strate within 2 weeks, and the isopods fed on this growth. Thereafter, food was supplied only when algae seemed sparse or absent.

Isopods used in experiments were measured with calipers to the nearest 0.5 mm. The length of the body was multiplied by the width at its midpoint to obtain the approximate surface area of each individual in square millimetres. Isopods were observed in the field for over 220 h and in the laboratory for over 280 h.

Experiments
Female Size–Fecundity Relationship

Brood size is proportional to female body size in many isopod species (Hatchett 1947; Ellis 1961; Steel 1961; Jones & Naylor 1971; Carefoot 1973; Lawlor 1976). Manning (1975) has demonstrated male mate discrimination on the basis of female body size (and thus on the basis of fecundity) in the freshwater isopods *Asellus aquaticus* and *A. meridianus*. In this experiment I wished to determine if brood size is proportional to female body size in *T. thermophilum*.

Methods. Forty-one gravid females were isolated from samples taken in the summer of 1978. Females were placed in individual chambers constructed of 75 × 100-mm fine-mesh nets and suspended in aquaria. The females fed primarily on algae that grew on the nets. Vegetable food was supplied as described above. Upon their release from the marsupium, I separated the young from the females, counted them, and then used linear regression to identify the relationship between female size and fecundity.

Results. Brood size correlated positively with female body size ($r = 0.847$, $P<0.001$, $N = 41$; Fig. 2). Females in this sample ranged in size from 8.0 to 42.75 mm^2 ($\bar{X}\pm$SD $= 18.31\pm7.36$ mm^2). Brood sizes ranged from 3 to 57 individuals ($\bar{X}\pm$SD $= 15.48\pm11.41$).

Male Discrimination of Female Body Size

Since fecundity is proportional to female body size, males should discriminate against small females. The fact that males retain some females and release others suggests that males discriminate using some criteria. In this experiment I hoped to determine whether males discriminate female body size when selecting mates.

Methods. Nineteen large, mature males (69.00 to 87.50 mm^2) and 60 mature females (12.25 to 38.25 mm^2) were removed from laboratory aquaria. As with most population samples, the size distribution among females was roughly tri-

modal (Shuster 1979). The approximate size groups of females were (A) 12.25 to 18.0 mm^2, (B) 19.5 to 28.0 mm^2, and (C) 30.0 to 38.25 mm^2. Females with conspicuous, yellow ovaries were assumed to be mature and receptive to males. Five such females representing the complete range of female sizes were placed in a large petri dish with a single male and observed. A stopwatch was started when the male began assessing a female. Rejected females were removed, measured, and replaced by another female of similar size (within 0.5 mm^2). Guarded females were separated from males, measured, and replaced by another female of similar size (within 0.5 mm^2). Males were replaced every 15 min to avoid the possibility of their recognizing and avoiding certain females. This step also prevented a few males from seriously inflating the number of rejections. The procedure was continued until 30 females had been rejected and 30 females had been paired. The maximum number of females rejected by one male was four. The maximum number of females guarded by one male was three. The effect of female size on male guarding and rejection behaviour was tested by comparing the sizes of paired and rejected females with a Mann–Whitney *U*-test. A similar design for determining male discrimination in the isopods *Asellus aquaticus* and *A. meridianus* was
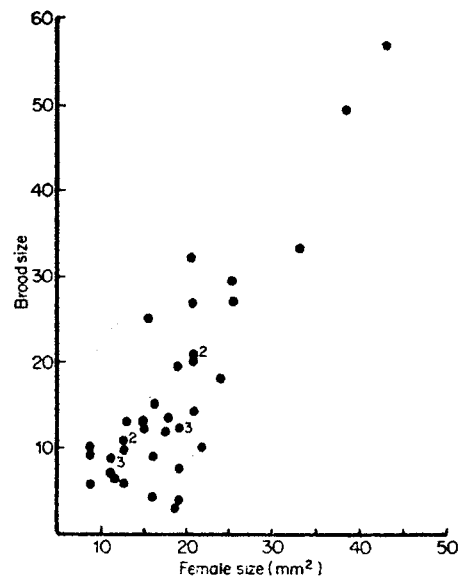
Fig. 2. Relationship between female size and fecundity. Numbers beside points indicate the number of same-sized females producing same-sized broods ($r = 0.847$, $P < 0.001$, $N = 41$).

used by Manning (1975). To determine whether males discriminate female body size within the size groups A, B, or C, the sizes of paired and rejected females within these groups were compared using a Mann–Whitney U-test.

Results. Males initiated precopulatory guarding significantly more frequently with large females than with small females (Mann–Whitney U-test, $P<0.005$; Fig. 3). However, males did not discriminate female size within size groups A or B (Mann–Whitney U-test, $P \geq 0.20$, Table II).
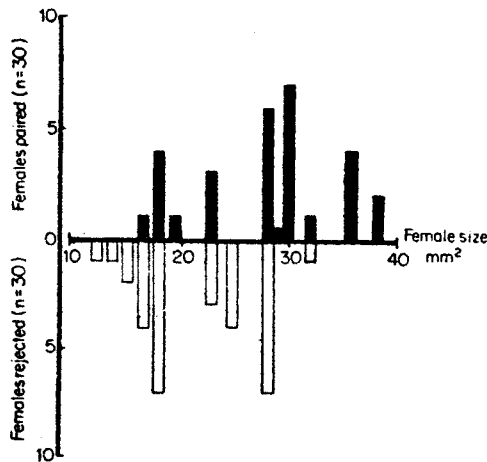

Fig. 3. Relationship between female size and the initiation of guarding behaviour by males. Dark bars represent females guarded; light bars represent females rejected. Guarded females were significantly larger than rejected females (Mann–Whitney U-test, $P < 0.005$).

Since only one female was rejected in group C, statistical analysis could not be performed on this group.

Male Discrimination of Female Reproductive Condition

Female receptivity associated with moulting is common in crustacea (Barnes 1974). Males in these species might therefore discriminate female reproductive condition in relation to the nearness of this moult because near-moult females could offer high fertilization rates to males. In this experiment I wished to determine the effect of female reproductive condition in relation to a sexual moult on male precopulatory guarding and rejection behaviour in $T.$ $thermophilum$.

Methods. One hundred and ten females (12.5 to 36.0 mm²) and 41 large, mature males (69.0 to 91.0 mm²) were collected from laboratory aquaria. As in the previous experiment, females could be separated into the following size groups: (A') 12.5 to 18.0 mm², (B') 19.5 to 28.0 mm², and (C') 30.0 to 36.0 mm². Members of each size group were separated into reproductive phases 1, 2, or 3 as described on p. 700 (Table I). Keeping size groups separate, one female of each reproductive phase (1, 2, and 3) was placed in a petri dish with a single male. Since males do not appear to discriminate subtle differences in female size, segregation of size groups forced males to select females by reproductive phase alone. A stopwatch was started when the male began assessing a female. Each rejected female was removed and replaced by another female of the same size

Table II. Sizes of Paired and Rejected Females*

| | Size group (mm²) | | | | |
| A | | B | | C | |
Paired	Rejected	Paired	Rejected	Paired	Rejected
16.5	12.25	19.5	22.75	30.0	32.0
18.0	12.75	22.75	22.75	30.0	
18.0	15.0	22.75	22.75	30.0	
18.0	15.0	22.75	24.5	30.0	
18.0	16.5	28.0	24.5	30.0	
	16.5	28.0	24.5	30.0	
	16.5	28.0	24.5	30.0	
	16.5	28.0	28.0	32.0	
	18.0	28.0	28.0	36.0	
	18.0	28.0	28.0	36.0	
	18.0		28.0	36.0	
	18.0		28.0	36.0	
	18.0		28.0	38.25	
	18.0		28.0	38.25	

*The sizes of paired and rejected females for groups A and B are not significantly different (Mann–Whitney U-test, $P \geq 0.20$). Group C could not be statistically analysed.

group and of the same reproductive phase. The amount of time the rejected female was held by the male before being discarded was recorded. When guarding was initiated, pairs were removed and placed in a separate petri dish. A new female of the same size group and the same reproductive phase and a new male were placed in the petri dish with the other females. A total of 79 rejections and 31 pairings were observed. The maximum number of rejections by one male was nine; hence the total number of rejections may appear somewhat inflated compared to the total number of pairings. A G-test was used to determine the effect of female reproductive phase on male guarding frequency. A G-test was also used to determine the effect of female reproductive phase on male rejection frequency. I compared the times in seconds before rejection of females in the three reproductive phases by using a Kruskal–Wallis test to determine the effect of female reproductive phase on male guarding time before rejection. Note that rejection behaviour and guarding behaviour were tested separately.

Results. Males apparently discriminate female reproductive condition as shown in Table III. Males preferentially guarded phase 2 and phase 3 females, while phase 1 females were rarely guarded (G-test, $P<0.005$). Phase 2 females were guarded somewhat more frequently than phase 3 females, but this difference was not significant (G-test, $0.05<P<0.10$). There was no significant difference between the frequencies of rejections for females in each phase (G-test, Table III). Males did, however, reject some females sooner than others (Kruskal–Wallis test, $P<0.05$; Table III). Phase 2 females were held longest before rejection.

Male Guarding and Female Quality

Since male guarding times that result in high fertilization rates should evolve in species with precopulatory guarding (Parker 1974), females with many potential fertilizations should be guarded longer, or at least should be less readily abandoned by males than females offering few potential fertilizations. In this experiment I hoped to determine the effect of female reproductive condition on the distribution of male guarding time.

Methods. The pairs obtained from the above experiment were retained within individual petri dishes and observed. Each petri dish was supplied with food (Tetra-min) and a crumpled piece of paper towel for shelter. Petri dishes containing food and isopods frequently went anoxic when incubated. Thus the temperature in the petri dishes was maintained at 28 C, somewhat below the water temperature recorded at the origin of Sedillo Spring (31 to 33 C) but within the range of temperatures encountered by this species (Shuster 1979). The frequency of male guarding was recorded daily until each female became gravid. The effect of female reproductive phase on male guarding persistence was tested as follows: (1) the longest periods of guarding (in days) for males possessing females in phases 2 and 3 were compared using a Mann–Whitney U-test; (2) among males that began their longest period of guarding immediately after being placed in the petri dish, the number of males guarding phase 2 females was compared with the number of males guarding phase 3 females using Fisher's Exact test. Since males discriminated against phase 1 females in the previous experiment (only two such females were guarded), phase 1 females were not included in statistical analyses.

Results. Males frequently abandoned females in all phases (1, 2, and 3) before females became gravid. There was no significant difference between the longest periods of male guarding for females in phases 2 and 3 (phase 2, range = 1 to

Table III. Male Discrimination of Female Reproductive Condition†

| | Reproductive phase | | | | |
	I	II	III	Test	Value
Females guarded	3	17	11	G	10.95**
Females rejected	34	24	21	G	3.50
Median time before rejection	30.0	77.7	31.5	Kruskal–Wallis	6.02*

†Values significant at the 0.05 and the 0.005 levels are indicated by one and two asterisks, respectively. The unmarked value is non-significant at the 0.05 level.

10 days, median = 2 days, $N = 15$; phase 3, range = 1 to 7 days, median = 1 day, $N = 10$; Mann–Whitney U-test, $0.05 < P < 0.10$). However, males guarding phase 2 females began their longest period of guarding immediately after confinement with such females significantly more often than males guarding phase 3 females (Fisher's Exact test, $P = 0.05$).

Male Size and Guarding Ability

When male competition for mates is intense, guarding males should leave areas of high male density to avoid usurpation by single males (Parker 1974). Male sequestration of females beneath the substrate or in cavities is probably an example of this sort of emigration. If males are unable to sequester females, only males with superior guarding and usurping ability should consistently obtain mates. In this experiment I investigated male guarding ability when sequestration sites are lacking.

Methods. Twenty mature males (31.5 to 91.0 mm²) and 10 mature females (12.5 to 18.0 mm²) with conspicuous ovarian development were collected from laboratory aquaria. Males were separated by size into five groups that represented the size range of sexually mature males (see Table IV). Two males from each size group ($N = 10$) and five mature females were placed in one of two 35-litre aquaria. This created high male density with variance in male size and low female density. Since the females were all of similar size and reproductive condition, all females were assumed to be similarly attractive to males. The aquaria contained no substrate and water temperature was maintained at 31 C.

Guarding males were removed, separated from the females, and measured, and then both individuals were returned to the aquarium each day for 21 days. Each week all males and females were removed and examined. Males that had moulted and grown were replaced by males of the original size group. Females that had become gravid were replaced by similar-sized females

with conspicuous ovaries. A G-test was used to determine whether all male size groups were equally capable of guarding females.

Results. Males in the largest size group were significantly more successful at obtaining females and guarding them than were males in smaller size groups (G-test, $P < 0.001$, for both aquaria, Table IV).

Male and Female Body Size among Sequestered Pairs

As a control for the previous experiment, I wished to determine whether males of a variety of sizes could secure mates when sequestration sites were provided. In addition, since males preferred large females as mates, and large males are superior sexual competitors, I wished to identify the relationship between male and female body size among sequestered pairs.

Methods. All sequestered pairs ($N = 54$) were removed from the substrate of three aquaria. Pairs were separated and each individual was measured. Spearman's rank correlation procedure was used to identify the relationship between male size and female size among pairs.

Results. Males possessing mates ranged in size from 28.0 to 87.75 mm² ($\bar{X} \pm \text{SD} = 61.1 \pm 17.0$ mm²). Guarded females ranged in size from 11.25 to 36.0 mm² ($\bar{X} \pm \text{SD} = 21.38 \pm 5.8$ mm²). Guarded female body size correlated positively with guarding male body size ($r_s = 0.709$, $P < 0.001$, $N = 54$). The above data are plotted in Fig. 4 ($r = 0.689$, $P < 0.001$).

Discussion

Fecundity is positively correlated with female size in *T. thermophilum*, and males preferentially guard large females. Males selectively guarding and inseminating such females should achieve higher fertilization rates than males guarding and inseminating small females. Assessment of females by males includes leg movements along the female's body, which are accomplished while

Table IV. Male Size and Guarding Ability with Low Female Density*

	Male size (mm²)	91.0–81.25	81.0–69.0	66.0–65.0	60.0–50.0	45.0–40.5	33.75–31.5
Number of guarding males	Aquarium 1	14	NA	0	1	2	0
	Aquarium 2	NA	15	4	2	5	0

*G-test: $P < 0.001$ for both aquaria.

the male rests on his dorsal surface. Turning and hefting a female may allow males to 'estimate' female size. Males apparently do not, however, detect subtle size differences among females. Thus males might discriminate among females by comparing the size of the previously encountered female with the one presently 'at hand'. If the previous female was the same size or larger than the present female, the male might continue searching. If the previous female was smaller than the present female, the male might discontinue searching and begin guarding, provided that the present female satisfies other criteria for male choice. Such a mechanism does not require that males possess long-term memories or the ability to determine accurately individual female size to obtain large mates (J. F. Downhower, personal communication).

Males discriminated against females that had not undergone a sexual moult (phase 1), and showed a preference for near-moult females (phase 2) over postmoult females (phase 3) in choice tests. Males also abandoned phase 3 females sooner than they abandoned phase 2 females. This finding agrees with earlier speculation on male guarding behaviour in crustacea, but phase 3 females were somewhat more attractive to males than expected.
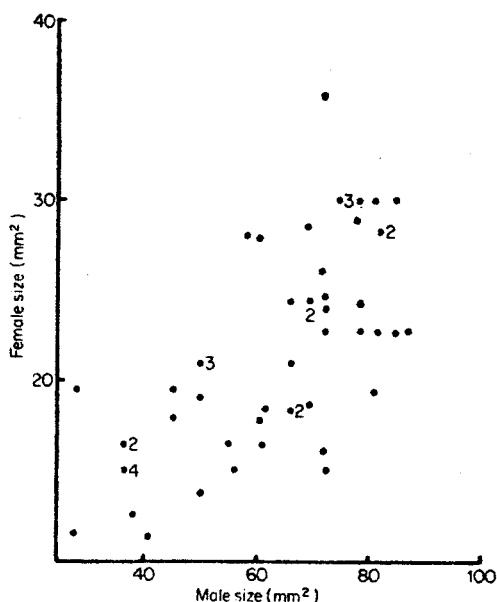

Fig. 4. Relationship between male body size and female body size among sequestered pairs. Numbers beside points indicate the number of same-sized females sequestered by same-sized males ($r = 0.689, P < 0.001, N = 54$).

Female sphaeromatids often lack sperm-storing diverticulae such as insect spermathecae (Menzies 1954; Holdich 1968; Venkatakrishnan & Nair 1973); thus the ejaculate of the first male to mate may be closest to the female's ovaries and may fertilize more ova than subsequent ejaculates. This system could select for precopulatory guarding behaviour by males as suggested by Parker (1974), and may explain the particular attractiveness of phase 2 females to males. The configuration of female reproductive tracts might also prevent sperm competition if sperm mixing is minimal. Female ability to resist copulation could delay insemination for some time and thus may explain female attractiveness long after a sexual moult (e.g. phase 3 females). Alternatively, if ejaculates mix, the amount of time required for males to accomplish insemination and the potential for sperm competition in previously mated females should determine the attractiveness of postmoult females. However, sperm competition should select strongly for postcopulatory guarding by males, and I have not observed males retaining females for significant lengths of time after insemination. I am presently investigating the nature of sperm competition in this species.

While sexually mature males vary in size, large males are superior sexual competitors and, as with most crustacea, large males are old males (Barnes 1974). Females should prefer large, old males because such males have demonstrated survival and food-gathering abilities not demonstrated by small, young males. Genes associated with survival and feeding (not necessarily genes specifically related to size) could be transmitted to offspring and increase female reproductive success. The greater reproductive success of males surviving long enough to attain large sizes has probably contributed to the sexual dimorphism observed in this species.

Both sexes should prefer large mates, but small males may be unable to retain large females in male–male competition, and large females may reject small males because such males have not demonstrated their genetic fitness. Mechanical inability of small males to inseminate large females is unlikely because selection should favour males able to inseminate any mature female (given the opportunity), regardless of the size of either participant. Males should favour large females over small females unless small females require less guarding time than large females. If small females are more compliant than large females, more large males should have been found guarding small females. Females close to a

sexual moult might require approximately the same amount of time to shed their cuticle, and thus may require similar guarding time before insemination is possible. Large males should therefore mate with small females only if large females are unavailable. Small females may be restricted to mating with small males and vice versa.

Females apparently discriminate among potential mates by rolling up. Since males should attempt to maximize their frequency of contacts with receptive females, reluctant females may not have to wait long to be abandoned. Chemical or acoustical rejection mechanisms of females are therefore not likely to have evolved. Rolled-up females may minimize their risk of injury during male assessment or during usurpation attempts by single males. This behaviour may also make females difficult for males to handle, forcing guarding males to be conspicuous, increasing male–male competition and thereby increasing a female's chances of obtaining large males as mates. Female ability to resist insemination might reduce the possibility of sperm competition in this species.

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